

Anatomy of a complex trace fossil: *Phymatoderma* from Pliocene bathyal mudstone, northwestern Ecuador

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Abstract. An exceptionally well-preserved example of *Phymatoderma granulatum* from continental slope deposits within the Pliocene Upper Onzole Formation, coastal Ecuador, supports an important reinterpretation of this large, branching, subhorizontal burrow system. Traces such as this have been regarded simply as fodinichnia (the work of subsurface deposit feeders). However, we propose that the trace producer was capable of changing its feeding strategy as a probable adaptation to a variable trophic regime. Tunnels within the burrow system are filled with pelleted volcanic ash conveyed from the seafloor to subsurface storage areas, indicating surface deposit feeding; the same tunnels enclose secondary tunnels that rework the primary fill of pellets, pointing to recycling/restocking of fecal banks as another trophic behavior. Alternative feeding strategies represented in *P. granulatum* could be the reactions of the burrowing animal to a pulsed delivery of labile organic material at the ocean bottom (in this instance associated with large ashfalls).

Key words: Continental slope, deepsea paleoecology, Ecuador, ethology, *Phymatoderma*, Pliocene

Introduction

Unique, well-preserved fossil specimens have always been crucial in paleontology for working out the details of anatomy, function, ecologic properties, and genealogic relationships of every kind of organism, from protist to dinosaur. A newly discovered specimen, having all the skeletal elements intact, appendages still attached or the soft tissues preserved, is often more important than all the fragmentary remains of a particular species (or higher taxon) ever collected. The same thing is true for trace fossils: exceptional preservation can lead to breakthroughs in behavioral and ecologic interpretations.

In this paper we describe an exceptional example of *Phymatoderma granulatum* (Schlotheim, 1822) from Pliocene continental slope deposits of Ecuador (Figure 1), a specimen that allows a more comprehensive interpretation of this biogenic structure than was previously possible. *Phymatoderma* [identified by most authors as "Zonarites", "large *Chondrites*", or "pellet-filled *Chondrites*" (see Seilacher, 1954, 1958; Simpson, 1956; Sellwood, 1970; Chamberlain, 1977; Brenner and Seilacher, 1978; Pickerill *et al.*, 1984; Savrda and Bottjer, 1989; Savrda *et al.*, 1991)] is a distinctive, subhorizontal, branching burrow system consisting of clusters of radiating tunnels that converge and overlap near the center of the system. Such structures have been interpreted as fodinichnia (burrows produced by subsurface food-mining activity). However, we can show that the organism that produced the Ecuadorian specimen was

involved in more complicated behavior than simply subsurface deposit feeding, and apparently was capable of changing its feeding behavior and controlling its trophic resources to some extent. Although traditional methods of description and structural analysis can be applied to such intricate burrow systems, the traditional ethologic classification of trace fossils does not accommodate this kind of behavioral complexity. This paper supports and extends previous work by Miller and Vokes (1998) on the same trace fossils.

The example of *P. granulatum* described and illustrated here has been deposited in the University of California Museum of Paleontology (UCMP 39901).

Geologic context

The example of *P. granulatum* that we document was part of a moderately rich ichnofauna occurring in green mudrocks of the Pliocene Upper Onzole Formation, exposed near the coastal city of Esmeraldas (Figure 2). Visible in extensive wave-cut platforms and seacliffs at Punta Gorda (Figure 3), the formation consists of over 300 m of mostly thick-bedded mud turbidites with mud pelagite, silt-sand turbidite, and comparatively light-colored volcanic ash interbeds. The ichnofauna is preserved at the tops of the mud turbidite beds. Other common ichnotaxa in the Upper Onzole at this location include *Alcyonidiopsis* ichnosp., *Chondrites intricatus*, *Phycosiphon incertum*, *Rorschachichnus amoeba*, and *Zoophycos* ichnosp. The ichnofauna has been described recently by Miller and Vokes (1998).

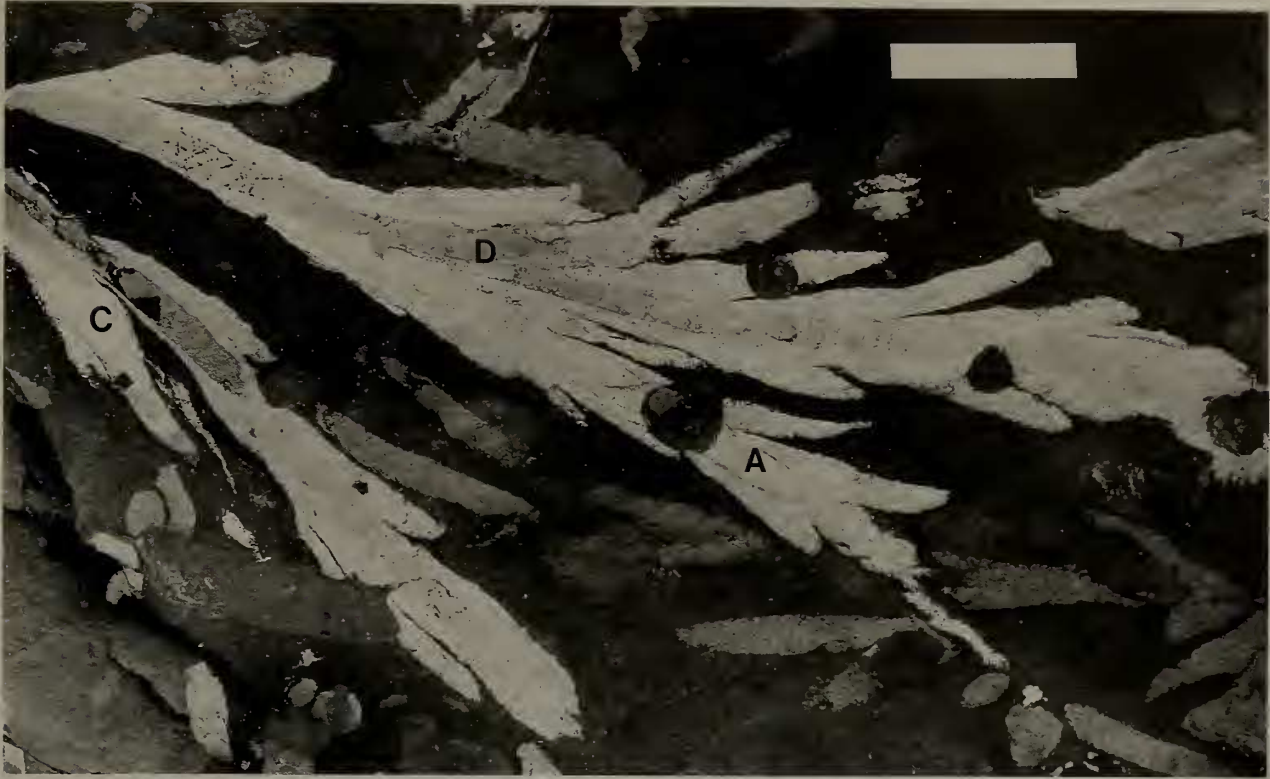


Figure 1. A large, well-preserved example of *Phymatoderma granulatum* from the Pliocene Upper Onzole Formation of northwestern Ecuador (UCMP 39901). Letters indicate locations of close views shown in Figure 5. Scale bar represents 4 cm.

Where the burrow systems occur below a volcanic ash, overall form and internal structure of the trace fossils have been preserved in extraordinary detail (Figures 4, 5). In this situation, burrows were filled either passively or by the trace producers actively conveying ash to subsurface tunnels or galleries, resulting in an ichnofauna that stands out in sharp contrast to the dark-colored matrix (Figures 1, 4B, 5). *Alicyonidiopsis*, *Zoophycos* and *Phymatoderma* all contain pellets made of the ash, indicating active filling of below-surface storage areas and suggesting that food caching or storage of fecal pellets was an important aspect of the behavior of animals that produced these varied structures. Kotake (1989, 1991, 1993, 1994) has described a strikingly similar pattern of ash-filled burrows occurring in Plio-Pleistocene bathyal deposits of Japan.

Mudrocks of the Upper Onzole Formation were deposited for the most part during planktic foraminiferid zones N. 19 and 20 (ca. 3–5 Ma), at bathyal depths on the inner trench slope (Evans and Whittaker, 1982; Whittaker, 1988). Aalto and Miller (*in press*) have proposed a trench-slope basin as the most likely depositional setting (Figure 2B). The basin received sediment chiefly in the form of successive, large-scale, muddy turbidity currents. Benthic ecosystems were continually reestablished on each newly deposited mud blanket; endobenthic populations produced distinctly tiered ichnoassemblages following recolonization (Figure 4A), of which *P. granulatum* is the most prominent component (Fig-

ure 4B). Thus, the Upper Onzole trace fossils represent the benthic ecosystems that existed in the basin "between" episodes of disturbance caused by the turbidity currents.

Paleoethologic classification and analysis

We are accustomed to the practice of equating an ichnotaxon to a single ethologic category or to one kind of organism-environment interaction. Most ichnologists employ the ethologic classification originally proposed by Seilacher (1953, figure 6), and subsequently modified to include additional categories (Ekdale *et al.* 1984; Frey and Pemberton, 1984; Ekdale, 1985; see recent summary in Bromley, 1996), to label the modal or most obvious behavior deduced for a particular biogenic structure. This classification has produced satisfactory results when applied to structurally simple traces that are essentially snapshots of a dominant habitat interaction or behavioral reaction, and has been used successfully in the analysis of stratigraphic successions and paleoenvironmental trends (Ekdale *et al.*, 1984; Pemberton, 1992). There have been problems created, however, by over-extending the scheme.

One unfortunate result has been to associate an ichnogenus (e.g., *Zoophycos*) exclusively with one of the standard ethologic categories (e.g., fodinichnia), even though the structures identified with that name could have been made at different times during the Phanerozoic by different kinds of

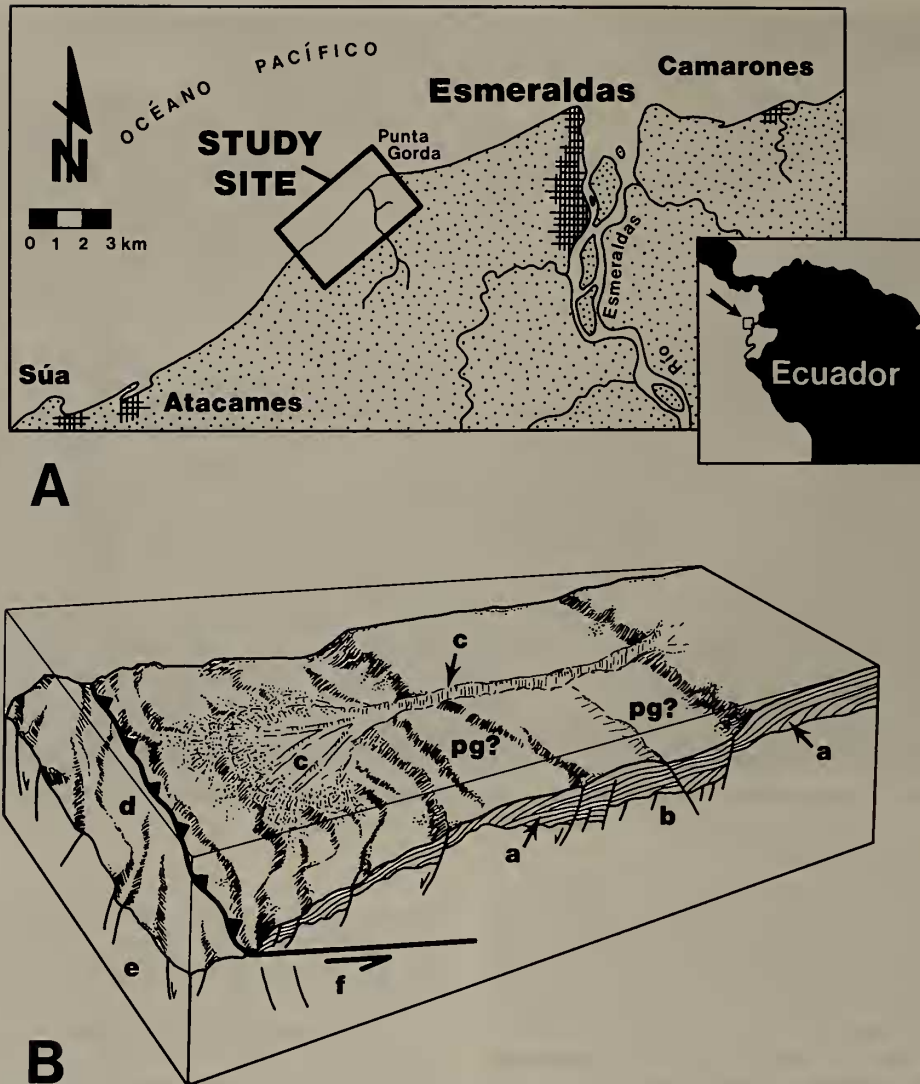


Figure 2. Location and paleogeographic reconstruction of the study site. (A) Location map. (B) Reconstruction of Pliocene continental margin of the Esmeraldas area showing possible position of study site on the inner trench slope (pg), Neogene trench-slope deposits and inboard equivalents (a), normal faults (b), Esmeraldas canyon-fan system (c), trench floor (d), oceanic crust (e), and subduction zone (f). Not drawn to scale; from Aalto and Miller (in press).

animals, possibly for different purposes. A more significant problem comes from the reevaluation of structurally elaborate traces (e.g., *Zoophycos*, *Paleodictyon*, *Ophiomorpha-Thalassinoides*, and other compound systems). These intricate burrow systems record long-term occupation in some cases (Bromley, 1996); variable behavior and possibly some form of habitat restructuring [including control of local environment, damping of disturbances, and active management of food supplies (see Hansell, 1984; Vander Wall, 1990; Jones *et al.*, 1994)]; and "extended phenotypes" of the trace producers affecting their survival and fitness (Dawkins, 1989). Such animal artefacts contain evidence of complicated behavioral routines and subroutines involved in

the construction, operation and maintenance of the structures. In this view, they are comparable to complex terrestrial artefacts like beaver dam-lodge-impoundment systems and termite "nests".

The traditional ethologic classification was not intended to accommodate this kind of complexity. Miller (1996a, b, 1998) has proposed that intricate biogenic structures preserving evidence of complex behavior, including some control of local environments, should be designated as "deliberate" trace fossils and receive special attention as rich sources of paleoethologic data; simpler, "incidental" structures (typically short-lived and preserving evidence of one kind of behavior or reaction) can still be accommodated in the

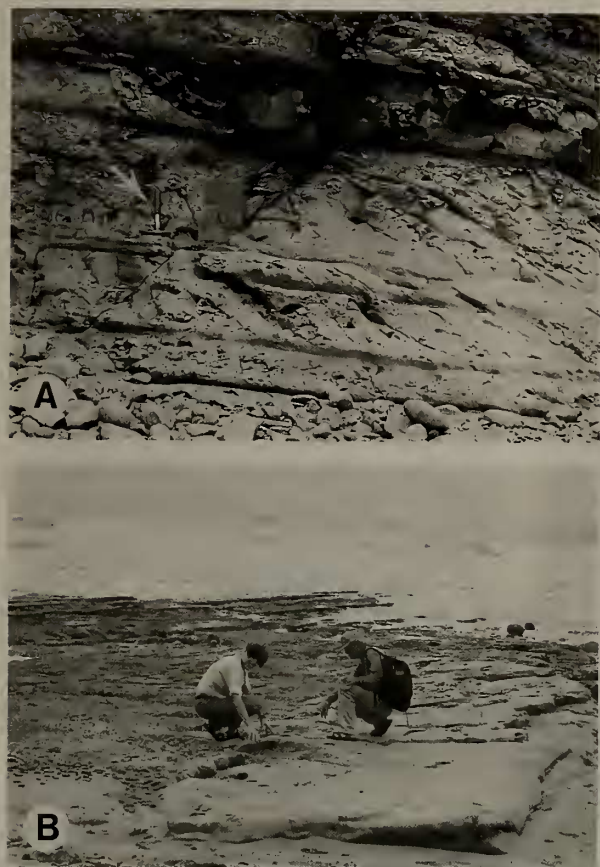


Figure 3. Punta Gorda outcrops of the Upper Onzole mudstone. (A) Seacliff consisting of thick muddy turbidites (hammer at arrow is 25 cm long). (B) Intertidal platform showing large, gently-dipping bedding surfaces (S. Walker and F. Cortez for scale).

traditional classification. *Phymatoderma granulatum* is a complex burrow system and belongs in the former general category.

Paleoethologic analysis depends upon two sources of information: "morphology" (really a structural inventory) of trace fossils, and comparison with modern traces or trace-producing activity. This approach can be termed the "actualistic method" (reviewed in Seilacher, 1953; Schäfer, 1972; Frey, 1975; Frey and Seilacher, 1980; Ekdale *et al.*, 1984; Frey and Pemberton, 1985; Pemberton, 1992; Bromley, 1996). The fundamental idea behind this form of analysis is that a fossilized "token" of behavior (e.g., branching pattern, wall structure, or the organization/composition of fill material of burrow systems) potentially can be matched to a modern structure produced by a particular kind of organism, or to a behavioral product made by different organisms having broadly similar adaptations. In cases where uniformitarian assumptions are tenuous or unsupported (as with interpretation of Vendian traces or with structures having unknown modern counterparts), description of structural elements, overall morphology, and size, together with very general comparison to trace-producing activity of modern



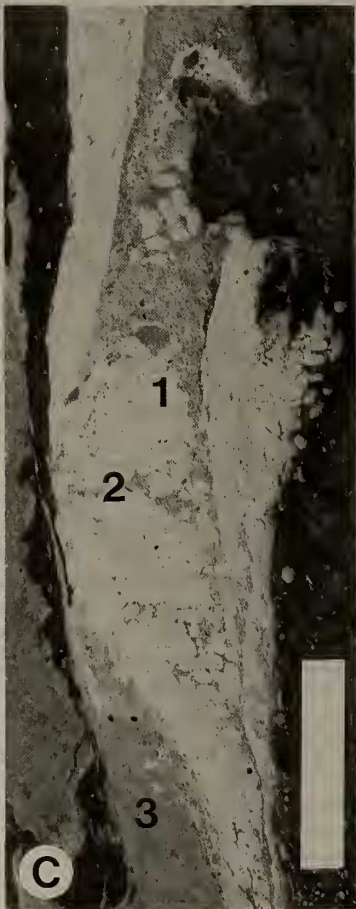
Figure 4. Punta Gorda trace fossils. (A) Tiered ichnoassemblage below a volcanic ash (a), with *Phymatoderma* (p) as the most prominent shallow burrow system and *Zoophycos* (z) as the deepest system. (B) Dense cluster of *Phymatoderma* on a bedding surface (field of view is approximately 0.5 m wide).

organisms, still can yield plausible interpretations of biogenic structures. This is the method we have employed.

It is important to keep in mind that structural intricacy is related to behavioral complexity. The more complicated and varied the tokens of burrow fabrication, the more complicated is the behavior required to build, operate, and maintain a particular structure (Hansell, 1984; Dawkins, 1989). Thus, the behavior "visible" in a specimen of *Skolithos* or *Planolites* is simpler than that in *Zoophycos* or *Paleodictyon*, notwithstanding the fact that the entire behavioral repertoire of the trace producers is only partially recorded in these different structures. The obvious, but largely unappreciated, point to make here is that demonstrably complex structures are the records of complex behavior.

Ecuadorian *Phymatoderma*

General features: In the Punta Gorda exposures, *Phymatoderma granulatum* is a shallow-tier burrow system



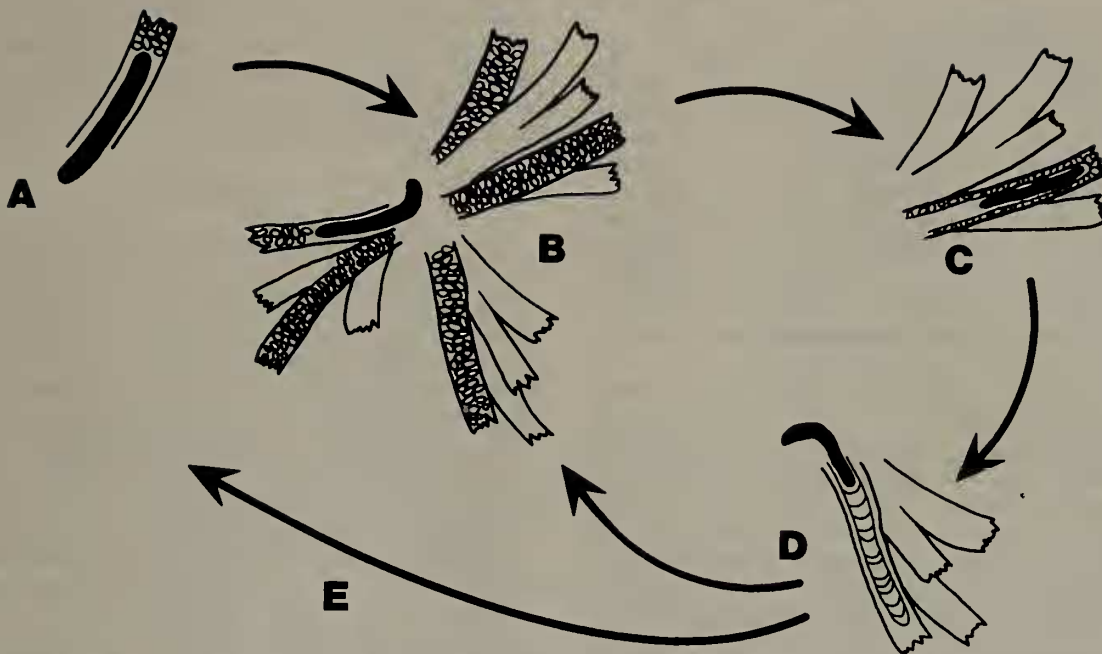


Figure 6. An "action cartoon" depicting the fabrication of Ecuadorian *Phymatoderma*. Successive parts include (A) initiation of structure, (B) construction and stocking of multiple tunnel bundles with pellets, (C) recycling of burrow contents, (D) withdrawal, and either (E) abandonment or (B again) restocking of structure. Only the most general features are shown.

occurring as clusters of large specimens (Miller and Vokes, 1998). The structures consist of bundles of radiating tunnels that overlap near the central region of the burrow system (Figures 1, 5). The tunnel bundles, or branches, extend outward 10 to 30 cm in typical specimens, but in a few instances the branches are >50 cm long. The branches themselves are organized in bundles that also diverge. Most of the structures were constructed at essentially one level below the seafloor; a few consist of multilevel systems. Estimated widths of the flattened tunnels vary from 3 mm to >1 cm within the same burrow system. Edges and terminations of tunnels are ragged, not uniformly smooth. Tunnels were originally unlined and filled with ellipsoidal pellets 1 to 2 mm in length.

These large burrows resemble some of the ichnospecies of *Chondrites*, but size, absence of uniformly smooth tunnel margins, subhorizontal orientation of the overall system, pelleted fill, and the overlapping tunnels allow recognition of *Phymatoderma* as a distinctive ichnotaxon. Fu (1991) has provided a taxonomic reevaluation of the ichnospecies of

Chondrites and *Phymatoderma*, and we have adopted her concept of *P. granulatum* here.

Conveyed material: The contrast in color between the light-gray volcanic ash filling the tunnels and the enclosing dark-green mudstone is perhaps the most striking feature of the Ecuadorian burrows. The nearly pure ash in many of the tunnels originally occurred in the form of pellets made of material conveyed from the seafloor to subsurface storage areas. However, the primary pelleted fabric has been obliterated by reworking and possibly compaction in many specimens. In the example we illustrate (Figures 1, 4), one can see the original pelleted fabric preserved at tunnel margins and extremities; most of the pellets are oriented with their long axes perpendicular to the tunnel margins. Well-preserved pellets are composed chiefly of ash, but sometimes contain crystal fragments and planktic foraminiferid tests that are pyritized in some cases. It is notable that although the surrounding mudstone contains a rich assemblage of both benthic and planktic foraminiferids (Hasson and Fischer, 1986; Whittaker, 1988), the ash-rich

Figure 5. Anatomy of an exceptional specimen of *Phymatoderma granulatum* (example shown in Figure 1). (A) Distal parts of tunnels packed with light-colored pellets. (B) A pellet made mostly of volcanic ash and containing a pyritized planktic foraminiferid test (dark dot). (C) Proximal part of branch showing secondary tunnel and the results of recycling/restocking burrow contents, including reworked ash areas (1), muddy laminae (2), and darker, muddy pellets (3). (D) Reworking of burrow fill in successive stages; earliest stage (1) is light colored with pelleted fabric preserved at the margins of tunnels, intermediate stage (2) consists of blotchy ash-mud mixture, and latest stage (3) is dark colored and cross-cuts all other internal structures. Scale in A and D marked in millimeters; scale bar in B represents 0.5 mm, and in C represents 1 cm.

portions of the burrow fills of *P. granulatum* contain almost exclusively planktic globigerinaceans.

Pellet composition indicates that the behavior of the trace producer included nonselective "surface" deposit feeding and the storage of fecal material or possibly caching of food-ash mixtures in subsurface tunnels. The trace producer lavished so much attention on the ash probably because ash deposition coincided with pulsed delivery of food to the ocean floor (discussed by Miller and Vokes, 1998). The overlapping, outward-branching tunnels, as in the traditional interpretation, suggest some form of subsurface deposit feeding as part of the organism's behavior. In addition, the primary pelleted fabric was apparently disrupted by the trace producer in a systematic way.

Secondary tunnels: Our example is typical of *P. granulatum* from the Punta Gorda beds in having secondary tunnels positioned in the middle of the pellet-filled primary tunnels. These subsequent tunnels rework the pelleted fill, but do not extend beyond the limits of the original structure. Earliest generations of the secondary tunnels contain apparently structureless, pure ash; the latest reworkings contain darker-colored ash-mud mixtures (Figure 5D). The reworked areas in some specimens have a meniscate structure with the concave sides of laminae oriented toward the central region of the burrow system. These laminae consist of interlayered ash and mud-rich sediment; in some of the tunnels the latest generation of reworked burrow fill also is pelleted, suggesting possible restocking (Figure 5C). Although a quantitative inventory of the foraminiferid component of the burrow fill was not performed, as it would entail destruction of the specimen, globigerinaceans also appear to be the dominant foraminiferids in the later ash-mud mixtures. Thus, the trace producers seem to have systematically revisited these storage areas to practice autocoprophagy/ utilize food caches and to restock tunnels with pellets.

Behavioral variability: This complicated pattern of burrow construction and utilization, over apparently long intervals of time (relative to life cycle of the trace producer), is evidence that the organisms responsible for *P. granulatum* could switch their trophic behavior from surface feeding (possibly in times of plenty) to other ways of feeding, including the reprocessing of pellet banks (in times of scanty food supply). This is precisely the behavioral adaptation required by relatively large, long-lived endobenthos exploiting a pulsed delivery of labile organic material to the seafloor (Jumars *et al.*, 1990). The seasonal or irregular supply of food to the deep ocean bottom, resulting from events such as plankton blooms, is now recognized as one of the most important processes controlling composition and structure of deepsea benthic ecosystems (reviewed by Gooday and Turley, 1990; Gage and Tyler, 1991; Smith, 1994). The pulsed delivery of food in this case was caused by, or coincident with, major volcanic ashfalls reaching the seafloor at the continental margin of northwestern South America (Miller and Vokes, 1998). Behavioral variability actually may have been greater than what we have suggested: initial construction of tunnels could have involved subsurface feeding and possibly the invasion of adjacent systems that were stocked with pellets; and repeated excursions into the pellet banks could have

promoted bacterial or fungal growth on pellet surfaces (a kind of passive cultivation; cf. Fu and Werner, 1995). At least we can say that *P. granulatum* records alternation of feeding strategies, and that surface deposit feeding and pellet recycling probably were essential behavioral adaptations of the trace producer.

Implications

The most popular way to illustrate behavior inferred from trace fossils is to use "action cartoons", showing organisms in the various stages of building and utilizing their burrows or borings (Miller, 1996a, b, 1998). In an action cartoon, Ecuadorian *Phymatoderma* would have to be depicted as the result of variable behavior, not one dominant kind of behavior (Figure 6). But in order to account for the structural intricacy more comprehensively, a much more complicated diagram of behavior is required (Figure 7). The detailed depiction of burrow-related activity in a blueprint or systems diagram of this kind has been termed fabrication analysis by Miller and Vokes (1998, fig. 11 and p. 38) and includes the itemization of "(1) construction (primary fabrication involving excavation, probing, lining and initial filling of structures); (2) operation (secondary fabrication including all forms of structure utilization and 'normal' modification after construction); and (3) maintenance (secondary fabrication involving minor localized repairs, reoccupation of damaged structural elements, extensions to the seafloor following catastrophic burial events, and reestablishment of structures after a major physical or biogenic disturbance". Simply stated, a diagram depicting the full range of possible behaviors recorded in *P. granulatum* would be a complex pattern in its own right, not a simple cartoon.

A more general implication from our study, as well as from other reevaluations of elaborate marine burrow systems, from new work on complex terrestrial trace fossils, and from a renewed interest in compound ichnotaxa, is that the traditional ethologic classification has important limitations (Miller, 1998). Complex animal artefacts are not easily accommodated in the traditional scheme (already demonstrated in the controversy over the behavioral interpretations of *Zoophycos*; Bromley, 1991). Such biogenic structures deserve special treatment individually as records of elaborate, variable behavior. Complexity of Ecuadorian *Phymatoderma* is apparently related to changing trophic resources, probably the result of pulsed delivery of labile organic material to the deep ocean floor. In this case, the pulsed delivery of food was associated with major ashfalls. By merely allocating our burrow system to a single, traditional ethologic category, we would have failed to recognize the essential behavioral and ecologic properties of the trace and the organism that constructed it.

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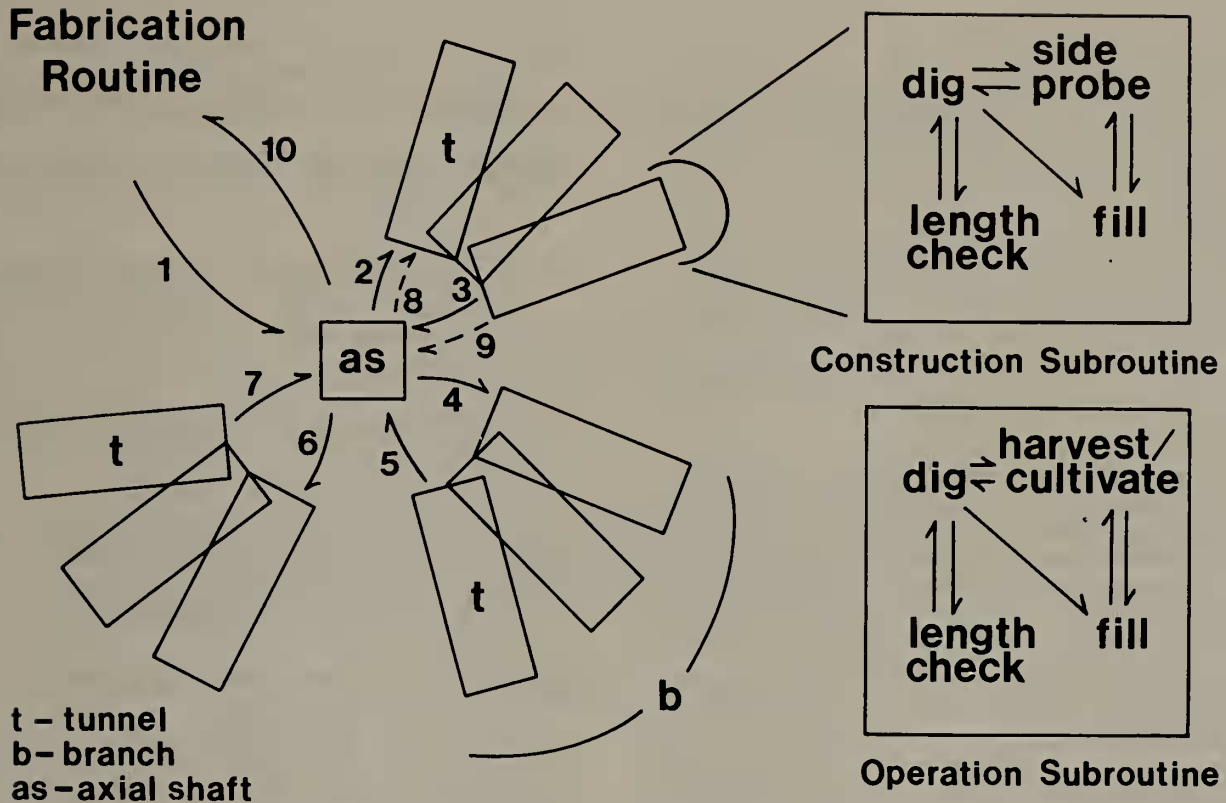


Figure 7. A possible blueprint of construction and utilization of Ecuadorian *Phymatoderma* that depicts burrow fabrication as a series of behavioral routines and subroutines—a more comprehensive summary than that shown in Figure 6. Fabrication sequence includes: (1) initiation of structure; (2–7) tunnel construction and stocking; (8–9) structural operation involving revisiting tunnels and recycling/restocking contents; and (10) abandonment. Structures such as this are demonstrably more complex (in terms of diversity of behavioral tokens) than simpler burrows that do not record long occupation, deliberate modification of habitat, and active management of food resources by the trace producer. From Miller and Vokes (1998, figure 11).

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